XV. *The Structure and Life-history of* Phalacrocera replicata. By Professor L. C. Miall, F.R.S., and R. Shelford, B.A. *With an Appendix on the Literature of the earlier stages of the* Cylindrotomina, by Baron C. R. Osten Sacken, Hon. F.E.S.

[Read April 7th, 1897.]

Plates VIII.—XI.

THE STRUCTURE AND LIFE-HISTORY OF *PHALACROCERA REPLICATA*.

1. *The forms and habits of the larva.*

The larva of this Dipterous insect is sometimes abundant upon submerged mosses or other aquatic plants. It is, so far as our experience goes, a very local species. Our supply, which we owed in the first instance to the kindness of Mr. Henry Scherren, came from marshes between Pevensey and Bexhill, where the larva feeds upon a moss, *Amblystegium exannulatum*.* Fragments of this moss are easily recognised by the microscope in the ali-

* Identified for us by Mr. M. B. Slater, F.L.S. Mr. Scherren gives us the following localities :—The Norfolk Broads (Hickling, Ormesby), the Waveney, near Beccles Bridge, marshes round Brightlingsea, Seaford. We have not found the insect in Yorkshire. *Phalacrocera* has been taken in France, Germany, and Sweden. It is said to feed upon *Hypnum elodes*, *Fontinalis antipyretica*, and other mosses, besides *Amblystegium* (formerly known as *Hypnum fluitans*).

mentary canal; they give a green tinge to young larvæ when seen through the semi-transparent body-wall, especially from the underside. Older larvæ are more opaque, and of a brownish-green colour, with a pale and indistinct striping; the ventral surface of such larvæ is white. Full-grown larvæ are about an inch long. They are distinguished at a glance from other Dipterous larvæ by the long, transparent processes, which stand out from every surface. The larva is extremely sluggish, remaining almost motionless for hours together. It clings to a moss-stem by its large anal hooks, and, thus secured, it may at times be observed to sway its body from side to side, as if to promote respiration. It creeps from stem to stem by grasping with the mandibles and the anal hooks alternately. When alarmed, it curls itself up like a caterpillar. Ecto-parasitic organisms, such as Algæ, Diatoms, and Infusoria, often attach themselves in great numbers to its skin, and especially to the outstanding processes. A small Planorbis has been found creeping upon it, and probably feeding on the vegetable growths. These parasitic organisms, together with the general colour of the body and the form of the numerous filaments, give the larva a strong protective resemblance to the moss among which it dwells. Even when held up against the light it is not easily distinguished from the leafy stalks of the moss, and in the darkness of a weedy pool it must be altogether invisible.*

De Geer, who gives a good account of all the stages of *Phalacrocera*, with many illustrative figures (Mém. Hist. Ins., vi., p. 351, pl. xx.), tells us that the larva can endure long and severe cold. Being obliged to shut up his country-house, he left four of the larvæ to the mercy of a Swedish winter. The water by which they were surrounded froze at once to a solid mass. On returning in the following May, De Geer found the ice melted and half-evaporated. Two of the larvæ still survived, and were able to creep about and devour fresh food. Before the end of May both of them pupated.

The head can be completely retracted into the first and second thoracic segments, and is usually so retracted,

* Mr. Scherren recommends the collector to pull out a mass of vegetation, and shake it over a piece of mackintosh.

except when the larva is feeding. The orifice of protrusion is a transverse cleft on the front of the prothorax. As usual in the retractile heads of Dipterous larvæ, the hinder part, or occipital region, is imperfectly chitinised, and excavated by deep notches. No eyes or eye-spots have been found. There is a pair of small and slender antennæ (figs. 8, 9). The mandibles are small, but strong, curved inwards at the tip, and furnished, as is not uncommon, with a fringe of setæ, which help to close the mouth-opening (fig. 5). They are not externally visible, being enveloped within the maxillæ, which form the most conspicuous appendages of the head (figs. 9, 10, 11). They appear on both dorsal and ventral surfaces, and consist of a number of sclerites, united by soft integument, and surmounted by small palps. The largest sclerites are ventral (fig. 11, *sc.*), and are furnished with brushes (*br.*), which flank the labium on either side. Internal to these are subulate organs (*so.*), which possibly represent the labial palps. The so-called labium is a transverse plate, armed with teeth along its fore-edge, against which the mandibles act (figs. 10, 11, 12). As in some other Dipterous larvæ, a second plate of similar outline overlies it (fig. 6).

The body of the larva consists of eleven segments, most of which are subdivided into annuli. The varying number of the annuli, and the fact that in several segments the dorsal and ventral annuli differ in number, show that their morphological value is slight. It may be added that they vary a good deal in different Dipterous larvæ. In the first three segments the annuli are ill-defined; there seem to be two dorsal and three ventral annuli in segments 2 and 3. Segment 4 has three dorsal (ill-defined) and four ventral; segments 5 to 10 four dorsal and five ventral; and segment 11 no dorsal and perhaps three ventral.

On the front surface of the prothorax is a large transverse cleft, the orifice of invagination of the larval head. Above the cleft, when the head is protruded, a thick lip shows itself, which disappears from view when the head is completely retracted. The lip is seen in sections to be a fold of the body-wall, which facilitates the protrusion and retraction of the head. Like the floor of the invagination beneath the head, its morphologically external surface is covered with close-set setæ.

The anus opens on the ventral surface of the last segment. It is surrounded by about eight radiating folds, which together form a large circular area (fig. 2), which at first sight suggests a sucker, though we have no reason to suppose that it is ever used as such. The folds are continued internally for a considerable distance into the rectum, part of the mucous wall of which is therefore ordinarily everted. The folds are capable of retraction.

The chitinous cuticle is unusually thick in most parts of the body. It is plainly divisible into two layers, an outer one, which is dense, shagreen-like, and composed of small scaly prominences; and a much thicker and softer inner layer, which stains readily (fig. 31). Microscopic examination of a larval skin cast during pupation shows that the inner cuticle is absorbed before moulting.

Numerous long processes stand out from all surfaces of the body. These are grouped in dorsal, lateral and ventral series.

Dorsal series (fig. 1). Segment 1 (prothorax) bears one pair, segments 2 and 3, each two pairs of simple processes. In all the succeeding segments except the last the arrangement is:—annulus 1, no process; annulus 2, no process; annulus 3, an unbranched process; annulus 4, a branched process. Segment 11 has only the branched process, and the branch is so small that it can only be seen by close examination; it is of solid chitin, and forms what De Geer calls the smaller pair of anal hooks.

Lateral series (figs. 1, 2, 4). Segment 1 bears one pair; segments 2 and 3, two pairs each, the posterior being rudimentary; segment 4, two unequal pairs; the other segments with the exception of the last, three pairs each, the middle pair being the longest. Segment 11 has only a rudimentary lateral process.

Ventral series (figs. 2, 4). Segment 1 has no ventral processes, but only a few setæ; segments 2 and 3 have each a pair of rudimentary processes near the middle line, and also a pair of long processes, which are almost as much lateral as ventral; segment 4 has a pair of rudimentary processes on annulus 1, a pair of short ones on 2, a pair of long ones, besides a short median one, on 3; segments 5–9 exhibit five ventral annuli, of which the last bears a short median process, while the others have only

a patch of scales in the same position; all the annuli except the first have a pair of lateral ventral processes, which increase in length and become more widely separated from the 2nd to the 5th annulus. The last or 11th segment has no ventral processes, except a median setose tubercle on the second of the two annuli which lie in front of the anus.

These large and numerous processes suggest a respiratory function, which is partly confirmed by the presence of a good-sized trachea, running along every one. In the branched processes there are, as De Geer remarks, two separate tracheæ, which diverge at the fork.

Sections through the processes show that they are covered by a cuticle of relatively enormous thickness, far exceeding the diameter of the contained tracheæ; it is dense and tuberculate externally, but less compact within, the generating epidermis coming nearly into contact with the generating layer of the trachea (fig. 31). So thick and solid a covering is not easily reconciled with the respiratory character of the processes. It will be seen from the description of the tracheal system that the larva has spiracles, and that it visits the surface occasionally to supply them with air.

The closest parallels that we know to the numerous and long appendages of this larva are found, not in any Dipterous larva, but in the Lepidopterous *Paraponyx stratiotata** and the Coleopterous *Chemidotus cæsus*.† Trichopterous larvæ too may bear filaments more or less like those of *Phalacrocera*.‡

The larva has no true limbs. The last segment bears a pair of large, curved anal hooks, which are strongly chitinised on the convex dorsal side (figs. 1, 2, 4). Near the base and on the concave side is a setose tubercle. The tip of the hook is bifurcate, and just beneath it is a small bunch of setæ. These hooks are constantly used for grappling and locomotion. The "small anal hooks" of De Geer are described in connection with the dorsal processes (p. 346).

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* De Geer, *op. cit.*, i., pl. 37.

† Schiödte, De met. Eleutheratorum.

‡ The insects quoted are all aquatic. The terrestrial larva of *Cylindrotoma* (p. 361) bears similar but shorter processes.

2. *The alimentary canal of the larva.*

The mouth and œsophagus present no unusual features. There is a large œsophageal invagination. A capacious cylindrical stomach succeeds, which extends to the middle of the eighth segment, where the four Malpighian tubules enter the alimentary canal, and the intestine begins (fig. 18*b*).

The transition from the epithelium of the œsophagus to that of the stomach is quite sudden.* At this point the longitudinal muscles, which were internal in the œsophagus, pass through the annular muscles, and become external.†

The epithelium of the stomach, especially in the neighbourhood of the œsophagus, exhibits many narrow-necked, rounded *protrusions*, which push through the striated hem into the lumen of the stomach, and at last become detached as spherical masses. The protrusions are finely granular, and stain well (fig. 22).‡

Certain enlarged cells which are particularly numerous near the beginning of the stomach, contain peculiar *granular masses* of spherical shape (fig. 23). The granular masses are highly refractive, and stain badly or not at all.§ A nucleus is sometimes visible in the same cell. The masses occasionally divide within the cell into three or four (fig. 23), but the nucleus undergoes no corresponding division. The granular masses are ultimately discharged entire into the cavity of the stomach.‖

We have no conclusive evidence as to the function of either the protrusions or the granular masses. The protruded spheres have, however, been traced into drawn-out layers of fibrous or glairy texture which invest the food, and we are inclined to believe that they yield the peritrophic membrane described below. The non-staining granular masses are perhaps stages in the formation of some digestive secretion.¶

* Cf. *Dicranota* (L. C. Miall, Trans. Ent. Soc. Lond. 1893, p. 245).

† Cf. Balbiani, Études sur Cryptops. Arch. de Zool. exp. (2), viii. (1890).

‡ See also *Dicranota* (*loc. cit.*, p. 243).

§ The *mucous* or *calyciform* cells of Balbiani are described as staining deeply and uniformly.

‖ Cf. *Dicranota* (*loc. cit.*, pp. 243, 244).

¶ Cf. *Dicranota* (*loc. cit.*, p. 244).

A *striated hem* (fig. 23) is present in the epithelium of the stomach, though it is often demonstrated with difficulty. The hem consists of close-set, short, and blunt processes, which superficially, at least, resemble the perforated (?) end-plates of the epithelium of the villi in Vertebrates.

The epithelium is regenerated by small cells at the base (fig. 23), which are often grouped in twos and threes (*Watney's buds*).*

A *peritrophic membrane*† is found here as in some (perhaps many) other Dipterous larvæ. It is a secretion of the epithelium, which encloses the food and keeps it from direct contact with the epithelium. In the *Chironomus* larva it is particularly firm and homogeneous, forming a distinct tubular membrane. In the *Dicranota* larva what appears to be the same thing is voluminous and irregular.‡ We think it probable that the peritrophic membrane originates in the protrusions described above. It persists throughout the stomach and a great part of the intestine. It is a singular circumstance that the peritrophic membrane should arise in quite different fashions in different insects. In the *Chironomus* larva, and probably in Lepidopterous larvæ, it is a perpetually renewed prolongation of the chitinous lining of the stomodæum; in Myriopods, various Dipterous larvæ, including *Phalacrocera*, and other insects, it seems to be a secretion of the epithelium of the stomach (Balbiani, *loc. cit.*, pp. 30–32). We can confirm Balbiani's account so far as relates to *Chironomus*.

The epithelium gradually changes its character in the different parts of the stomach. Near the œsophageal invagination it is slightly folded, and consists of tall, columnar cells, grouped in bundles. Protrusions and

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* Watney, Phil. Trans., 1877; Miall and Denny, The Cockroach, p. 122 (1886); Oudemans, Bijdrage tot de Kennis der Thysanura en Collembola, p. 54 (1887); Balbiani, *loc. cit.*, p. 54 (1890).

† The name is Balbiani's (*loc. cit.*, p. 32). The same author gives references to Plateau, Schneider, and other naturalists, who have described a membrane enclosing the food in the intestine. See also Cuénot, Etudes physiol. des Orthoptères, Arch. Biol. (2), xiv. (1896).

‡ I now think that the secretion poured out upon the food in the *Dicranota* larva originates in the stomach. L. C. M.

granular masses are frequent. Towards the middle of the stomach the epithelium becomes regularly columnar. There are no protrusions or granular masses, but a finely granular secretion is poured forth. Beyond this zone the epithelium becomes cubical, and the granular masses reappear. Protrusions also occur, though not so frequently as in the upper portion. Towards the lower end of the stomach the epithelium becomes thin and flat. The Malpighian tubules and the beginning of the chitinous intima of the proctodæum show that the stomach passes into the intestine at a place where there is no change in the diameter of the tube. In *young larvæ* there seem to be no granular masses in the epithelium, which is uniform and irregularly columnar throughout the stomach; Watney's buds are very numerous. In *starved larvæ* the epithelium becomes unusually folded, and the protrusions are frequent, while the granular masses and the secretion in the cavity of the stomach are more copious. The cell-outlines are less clear than usual, and the epithelial cells appear to be more distinctly grouped into bundles than in normal larvæ.

The *intestine* (fig. 18*b*) may be divided into two tracts, colon and rectum. In the beginning of the colon the muscular layer, and especially its annular fibres, gradually increase in strength, while the epithelium and chitinous intima become folded. A circular valve occurs at the end of this section of the colon. Then the muscular wall thins out again, and for a variable length the intestine becomes flexible and capable of dilatation. A considerable oval enlargement, filled with food, is often seen somewhere in this portion.* The epithelium beyond the muscular thickening is at first cubical, but gradually becomes thin and flat. At the beginning of the rectum the muscular wall again becomes thickened. The epithelium and chitinous intima are, as usual, strongly folded. The anus has been described above (p. 345).

Salivary glands (fig. 18*a*). A pair of convoluted salivary glands lie along the œsophagus and the beginning of the stomach. Large nucleated cells, which form a single epithelial layer, bulge into the narrow and irre-

* *Phalacrocera* illustrates the remark of Balbiani (*loc. cit.*, p. 71) that the folds of the intestinal epithelium vary with the phase of digestion.

gular cavity. The glands are widest behind, and here the lining epithelium almost disappears, so that the glands become converted into mere reservoirs; they taper forwards, and pass into ducts, which unite below the subœsophageal ganglion to form a slender common duct, which enters the floor of the mouth (figs. 10, 18*a*.)

Malpighian tubules (figs. 18*a*, 18*b*). There are four long Malpighian tubules, which open at the junction of the stomach and intestine. Each passes forwards nearly as far as to the œsophageal invagination, and then turns backwards, ending opposite the colon in a coiled extremity.

3. *The heart of the larva.*

The heart (fig. 18*a*,18*b*) lies in a pericardial space, which is cut off from the body-cavity (hæmatocœl) by the usual diaphragm. The pericardial cells and alary muscles present no uncommon features. In the hinder part of the heart are several pairs of valvular inlets. There is one feature of the heart which we have never met with in any other insect, nor do we know of a close parallel in any other animal. Two cellular cords lie free in the cavity, which they traverse from end to end. They are attached behind to the body-wall between the spiracles, and extend forwards as far as the brain. They are here and there attached to the wall of the heart by slender threads. The cords are cylindrical, and consist of a transparent, slow-staining substance, in which are imbedded innumerable quick-staining cells, with relatively large nuclei (figs. 24-26). The cells are irregular, and often branched; between them and towards the centre of the cord is an irregular but probably continuous cavity. We are inclined to think that this cavity is filled in the living larva with a fluid, perhaps with blood. Sections reveal the very unexpected fact that the cords are of epidermic origin, tubular extensions of the epidermis of the hinder end of the body. They appear to pass into the heart through a pair of openings in its posterior wall.*

In the pupa the cords become beaded, break up, and finally disappear altogether. The difficulty of investigating the details of the process is very great, owing to the

* Owing to the great transparency and delicacy of the wall of the dorsal vessel, the double opening which we have mentioned was not clearly seen.

small size of the dorsal vessel and the rapidity with which the cords break up. We have observed that during disintegration very minute filaments, or rods, project from the cord, as if they were about to become free and form some constituent of the blood. The nuclei also become free and escape into the blood, as we infer from their frequent occurrence at the critical stage in a nearly detached condition. In a young pupa the cords are almost the same as in the larva, while in a pupa approaching the time of final transformation, not a trace of the cords is to be found.

The observations next to be related may throw some light upon the nature of the cellular cords.

In a young larva there was seen, just in front of the rectum and close to the anus, a multicellular, vacuolated body of rounded, irregular form, which seemed to be continuous with the epidermis, to which it was attached by a narrow stalk. Similar bodies have been found projecting from the dorsal surface. They all lie in the body-cavity (hæmatocœl). Segmentally arranged and single œnocytes occur throughout the body of the larva. They are often attached by threads or stalks to the body-wall, and when disintegrating have been observed to give off many fine filaments, which perhaps pass into the blood. The nuclei are of enormous size, and contain many nucleoli. The protoplasm of the œnocytes includes a vast number of granules or corpuscles, with occasional vacuoles. A peripheral nucleus is sometimes found (fig. 32).

We have not been able to find a close parallel to the cellular cords in any other insect. Outside the class of insects we can only point to rather vague and distant analogies, such as the following :—

Certain Oligochæt worms possess organs which have been called *cardiac bodies* and *blood-glands*.* The Enchytræidæ sometimes possess a cellular rod which runs the whole length of the dorsal vessel, being attached to its ventral wall. Michaelsen, the discoverer of the structure, assigns to it a mechanical function, that of facilitating occlusion of the tube during systole, without extreme contraction of the wall of the vessel. It has been suggested, though apparently not proved, that this cellular cardiac body of the Enchytræidæ originated in a dorsal diverticulum of the œsophagus. If this is well-

* Beddard, Monograph of the Order Oligochæta, p. 77.

founded, the cardiac body cannot be morphologically similar to the cellular rods of *Phalacrocera*. The other blood-glands described in Beddard's "Oligochæta" are still more remote from anything that we have found in *Phalacrocera*.

A second case of doubtful resemblance is found in the elæoblast of Tunicates. We have to thank Prof. W. A. Herdman, F.R.S., for the following statement of the facts:—

"The elæoblast of *Salpa* has been homologized by various writers with the tail of a normal Ascidian. It projects from the ventral surface of the embryo near its posterior end, but is not exclusively epidermic. There is a central mass of irregular vacuolated cells, more or less (according to the species and age of the embryo) in process of degeneration, which is supposed by Salensky, Brooks, and others, to be notochordal tissue. But the internal structure is rather indefinite; it is very probably the degenerate representative of several tissues, and the elæoblast seems to be formed at least partially by wandering kalymnoblasts (follicle-cells which have immigrated into the embryo). A good deal of phagocytosis goes on in the elæoblast, and it becomes greatly reduced towards the end of embryonic life. A trace of it can sometimes be found in a young adult. It is difficult to trace any morphological connection between the elæoblast and the epidermic cords in the heart of *Phalacrocera*, though they may be physiologically comparable, since both exercise a nutritive function at a time of rapid tissue-formation."

Certain epithelia are known to be capable of resolution into substances which are sometimes, though not always, nutritive. In the secretion of milk, nuclei, filaments and oil-drops are liberated by the breaking up of epithelial cells.* Both cock and hen pigeons feed their young for some days after hatching, upon curdy masses formed out of the thickened and fat-laden epithelium of the crop.†

The epidermis of various Fishes, Amphibia and Inverte-

* Steinhaus, Die Morphologie der Milchabsonderung, Du Bois Reymond's Archiv., 1892, Suppt.

† Waymouth Reid on Pigeon's Milk. B. A. Report, 1894.

brates, contains scattered cells or collections of cells which may discharge mucus, fibres, and nuclei.*

All insects which have been anatomically studied seem to agree in the possession of numerous blood-cells, which may float in the blood as corpuscles, or form sheets and solid masses in the blood-cavities. The yellow œnocytes described by Wielowiejski,† the pericardial cells, and the fat-body, answer to this description. The pericardial cells and the fat-body are believed to be peculiar kinds of cœlomic epithelium, but the œnocytes arise from the ectoderm. In *Hydrophilus* groups of parastigmatic œnocytes have been traced to invaginations of the ectoderm.‡ Such structures may be rudimentary analogues of the cellular cords, which attain such an extraordinary development in the larva of *Phalacrocera*.§

Kowalewsky‖ finds that in certain Orthoptera (*Pachytylus, Locusta*) Malpighian tubules penetrate the heart, entering by the cardio-cœlomic apertures which he has described, becoming much convoluted, and ultimately reaching the pericardium through the cardio-pericardial apertures. Here the motive seems to be, not nutrition at the expense of the blood, but purification of the blood itself, for which a large surface of contact is equally necessary.

We must now attempt some physiological interpretation of the cellular cords in the heart of *Phalacrocera*. We do so in a very guarded manner, feeling the difficulty of the task, and the necessity of a more searching inquiry than we have been able to undertake. It seems to us unlikely that the cords of *Phalacrocera* serve any such purely mechanical function as is ascribed by Michaelsen (see above) to the cellular rod of the Enchytræidæ. Numerous and large nuclei would not be required in a tissue which has no more complex function than to stop up a cavity. Nor does any such mechanical

* Waymouth Reid, The Process of Secretion in the skin of the common Eel. Phil. Trans., Vol. 185 (1894), and authors there cited.

† Zeitschr. f. wiss. Zool., xliii., pp. 512–536 (1886).

‡ Graber, Biol. Centralbl., xi., pp. 212–224 (1891).

§ Weismann's "garland-shaped cellular cord" (Entw. d. Dipteren, p. 132, pl. viii., fig. 10) may possibly be a structure of the same kind. See also Pantel on *Thricion* larva (C.R., 1897, i., pp. 472, 580).

‖ C.R., cix., pp. 409–411.

interpretation throw light upon the disappearance of the cords in the pupa, or upon the resemblance of the cords to the stalked prominences found elsewhere in the hæmatocœl, and to the œnocytes. It seems to us much more probable that all the structures described yield corpuscles, filaments, or other living nutritive particles, which are discharged into the blood at a time when the rapid growth of new tissues calls for enrichment of the fluid.

In the cellular cords we have a mass of epidermic reserve-tissue, which projects far into the hæmatocœl, and into that part of it which becomes specialized as the heart. This is one more instance of that tendency of epiblastic and hypoblastic tissues to bulge into any intervening space, which has led to so much perplexity in the interpretation of so-called mesoblastic organs.

We have considered the possibility that the cellular cords may be an organ of internal secretion. There is no positive evidence known to us which points to any such conclusion, and the rapid disappearance of the cords during the pupal stage seems to tell strongly against it.

4. *The respiratory organs of the larva.*

There is one pair of spiracles, situated on the dorsal surface of the last segment, between the base of the dorsal process and the anal hooks. The larva is therefore *metapneustic*, as is nearly always the case with Tipulidæ. The skin about the spiracles can be retracted so as to form a deep recess, with which both spiracles communicate. The spiracle forms the outer end of an air-chamber, into whose cavity strong and close-set setæ project. Towards the surface the setæ become rod-like, and their inner ends are attached to a central plug. The structure is much the same as in the larva of *Dicranota*,* and in neither case have inlets for the air been discovered. In both larvæ, however, the spiracle is exposed at times to the air, and the tracheæ are filled with air. The renewal of the air seems to take place at night, when both *Phalacrocera* and *Dicranota* have been seen to push their spiracles out of the water. There are two main tracheal trunks, which run along the dorsal surface and give off branches. In most of the segments there is a

* Miall, Trans. Ent. Soc. Lond. 1893.

small cross-connexion at the level of the pericardial diaphragm. As usual in submerged Diptera the branches of distribution are scanty, but relatively large tracheæ pass to the long processes. (See p. 347.)

The *Phalacrocera* larva can endure long abstinence from fresh air. We have kept them alive for a fortnight in a bottle absolutely full of water. In boiled water the larvæ lived for five days, when the experiment was discontinued. When access to fresh air is cut off the natural sluggishness of the larvæ is increased, but no permanent injury results unless the experiment is greatly protracted. The larva can live long out of water.

5. *The nervous system of the larva.*

The ganglia are the brain, the subœsophageal, three thoracic and eight abdominal (figs. 18*a*, 18*b*). When the head is retracted, the brain and two, or even three, of the succeeding ganglia are enclosed within it; when it is extended to its utmost (about one-third being then exposed) it contains only the brain and subœsophageal ganglion.

According to Brauer's peculiar nomenclature the *Phalacrocera* larva has a true head, the *Chironomus* larva only a "kiefer-kapsel." Yet his system requires that *Chironomus* should have the true head, and *Phalacrocera* the "kiefer-kapsel." It is becoming plain that Brauer's classification of the Nemocera by larval characters is based upon an insufficient knowledge of the structure of the larvæ.

The first abdominal ganglion is commonly found in its own segment, the last abdominal in segment 10. Between the brain and the first abdominal ganglia the connectives are double; in the abdomen they are single.

A pair of small nerves issue from the brain, run along the dorsal vessel, and enter a pair of ganglia, which are closely applied to it (figs. 19, 20). These are connected by short nerves with a frontal ganglion and a recurrent nerve. The whole arrangement is very similar to what exists in the *Chironomus* larva, and the larva of the Crane-fly.* In the thoracic region paired nerves issue

* Hammond, Science Gossip, xi., p. 204 (1875).

from the connectives of the nerve-cord and unite in pairs to form ansæ, or loops, from which lateral "respiratory" nerves usually proceed to the adjacent spiracles. We have not traced these nerves in the fly; in the larva there are no thoracic spiracles.

6. *The reproductive organs of the larva.*

The ovaries (fig. 30) form a pair of cylindrical bodies, tapering to each end, which lie on either side of the beginning of the intestine. The ovary is invested by a thin fibrous sheath. It consists of a central cellular cord, which is excavated by a row of cavities, communicating with one another. The wall is drawn out into many projecting follicles (fig. 31), which are pear-shaped, with narrow necks. Each follicle encloses a group of large nucleated cells, one of which is probably selected to form an ovum, but this we have not seen.

Such an ovary is unlike that of most Insects, and resembles, at least superficially, the ovary of many Mollusca, such as the cockles.* Instead of a small number of long ovarian tubes opening nearly at the same place into a common oviduct, we find in *Phalacrocera* a great number of short, single-chambered, though many-celled follicles, which open at various points into a central tube. The eggs of which (as we suppose) only one ripens in each follicle, may pass direct from such an ovary into the oviduct, whereas in the other arrangement they can only be liberated a few at a time. The ovary of *Phalacrocera* seems to be adapted to the almost simultaneous discharge of all the eggs, while the more usual disposition is appropriate to the successive discharge of eggs during a much longer time. In such Diptera as we are familiar with there is a multitude of short tubes or follicles, though *Tachina* and some few others have a few long tubes instead.

The testes occupy the same position as the ovaries, but are much smaller (fig. 27). At first they are filled with closely packed nucleated cells (spermospores), which by division produce loosely packed spermatozoa (fig. 29). Ripe spermatozoa may be found in advanced larvæ.

* Lacaze-Duthiers, Ann. Sci. Nat., Zool., 1854.

7. *The development of the imaginal organs.*

As usual in Diptera Nemocera, the rudiments of the future legs and wings appear simultaneously as three dorsal and three ventral invaginations. The ventral invaginations give rise to legs; of the dorsal rudiments the prothoracic becomes the pupal respiratory organ, the mesothoracic the functional wing, the metathoracic one of the halteres. The homology of the pupal respiratory organ, whether tube or bunch of filaments, with a prothoracic wing seems to be evident, though such a wing is unknown in any recent insect. The Carboniferous Ephemeridæ seem to furnish the best example.

The invaginations for the antennæ of the fly extend from the larval antenna to the brain; the rudiments of the compound eyes form near their hinder ends. Paired labial invaginations (fig. 6) form beneath the œsophagus as good-sized oval projections, extending backwards into the larval head.

8. *The process of pupation.*

A larva kept in confinement pupated on Oct. 16th. Air-bubbles were seen to form upon the processes, and when these were detached by shaking, new ones appeared. The larva was thus made buoyant, and floated in a horizontal position at the surface of the water. Shortly before the larval skin opened the spiracles were exposed to the air. The skin split along the dorsal surface of the prothorax, and the white head-end of the pupa began to protrude. The tips of the pupal respiratory tubes were brought to the surface of the water, and the body took a vertical position in consequence of changed hydrostatic conditions. The abdomen was alternately flexed and extended until the larval skin was slipped off backwards. As soon as it fell off and sank, the pupa lay horizontally at the surface. The work of extrication occupied a quarter of an hour. The pupa was at first pure white, except for a pair of bright-red spots on the fourth abdominal segment. These spots, which can sometimes be seen before pupation through the larval skin, are due to a red pigment which forms in the fat-body; they appear in both sexes, but only show through the larval skin in male larvæ. Two hours after pupation the pupa

had taken a dark-green colour. The fly appeared on Oct. 27th, so that the pupal stage lasted eleven days, unusually long in comparison with other aquatic Diptera.* The cast pupal skin was found to be attached to a leaf of moss by the dorsal projections from the hinder abdominal segments.

9. *The pupa.*

The pupa differs strikingly from the larva in its habits. It is comparatively active, and moves when requisite by flexion of the abdomen. When laid on the hand, it wriggles about, bending its body almost into a circle. The usual attitude of the pupa is vertical, the prothorax with the respiratory tubes just reaching the surface of the body; the pupa maintains itself in this position by grasping floating weeds with its dorsal abdominal hooks. Considerable disturbance of the water does not cause it to loose its hold. The pupa is also found at times floating at the surface; if turned over, it recovers its ordinary position, which is necessary to respiration, by movements of the abdomen. Sometimes it descends to a fair depth from the surface by the help of the weeds. The pupa is asphyxiated by a submergence of six hours.

Its length varies from three- to four-fifths of an inch. Its general colour is greenish-brown; there is a darker band along the mid-dorsal line, besides a median and two lateral dark bands on the ventral surface. The body is flattened dorso-ventrally, and produced laterally into thin margins, as in the *Chironomus* pupa. A pair of respiratory tubes project from the prothorax, diverging strongly from each other. The sixth and eighth abdominal segments are provided with dorsal projections, which serve to attach the pupa, and to prop it up in such a position that the prothorax is out of the water; there are also ventral and terminal projections. The thoracic legs are short, not reaching beyond the third abdominal segment. Rows of black dots are found on the dorsal, ventral, and lateral surfaces, whose arrangement is shown in figs. 13–15.

* De Geer found that the pupal stage lasted only six days, and we have found the time variable according to the season and temperature.

The dorsal abdominal projections consist of one pair on the sixth abdominal segment, which are curved, pointed, and directed backwards, and of two pairs on the eighth, which diverge from each other. Of these last the anterior pair are directed forwards, and are finely serrated on both margins; the posterior pair are turned backwards, and are serrated only on the anterior margin. A chitinous thickening which surrounds the segment connects them all together. On the ventral surface of the seventh abdominal segment is a pair of short, straight, and pointed processes, directed obliquely backwards. The last segment of all terminates in four small processes, two dorsal and two terminal; the dorsal pair are short and pointed, the terminal pair somewhat longer and also pointed. The processes of the eighth segment seem to serve for attachment; those of the sixth segment for maintaining the erect posture. Most of the segments show a division into three annuli.

10. *The imago.*

The perfect insect usually emerges in April, but one or more later broods may appear. The males and females are about equally numerous. The fly is sluggish, and does not travel far from the pool in which it was reared.

11. *Egg-laying.*

A female fly was observed to lay her eggs in a piece of moss. She crawled over the moss, inserting the extremity of the abdomen into the axils of the leaves, until about sixty had been laid. The moss selected is submerged. The eggs are laid singly, and adhere slightly to the moss; they are dark-coloured, opaque, and spindle-shaped. The surface of the chorion is irregularly pitted. At one end is a rosette-like micropyle, which was found to be beset with numerous spermatozoa.

12. *Comparison with nearly allied insects.*

The larva of *Cylindrotoma distinctissima*, as described by Zeller,* bears some resemblance to that of *Phalacrocera*. Unfortunately it has not been anatomically studied.

* Isis, 1842, p. 808.

The larva is terrestrial, feeding upon the leaves of *Anemone nemorosa*, *Stellaria nemorum*, etc. It attains a length of nearly an inch, and is narrow, depressed, tapering to each end, and of grass-green colour. There is a slight dorsal ridge, from which a row of short, backward-directed fleshy spines projects; one spine in each segment exceeds the rest in length. There is a broad lateral margin, bearing very short processes. The tracheal tubes are externally visible in the hinder part of the body; they open by conspicuous brown spiracles. The head can only be partially protruded. Zeller remarks that the orifice of protrusion is employed as a sucker. There are eight pairs of ventral prominences, like the pseudopods of caterpillars, but without hooks, and one pair of longer, backward-directed processes, beneath the anus. The larva can hold on either by the head or the tail. The pupa fixes itself to stalks or leaves by the tail, which is still covered by the remains of the larval skin; it is flattened, greenish in colour, and provided with two short respiratory trumpets. The occurrence of spines or processes (much shorter, indeed, than those of the *Phalacrocera* larva) in the terrestrial larva of *Cylindrotoma* seems to indicate that these are not necessarily organs of aquatic respiration. A fuller description of the structure and life-history of *Cylindrotoma* is much to be desired.

The supposed larva of *Triogma* (p. 364) resembles that of *Phalacrocera* in coloration, in the retractile head, and in the presence of numerous spines. Its appearance is strongly protective, and even when imprisoned in a collecting-box, it was not easily discovered. The pupa was pale green, bore many spines on the abdomen, and according to De Rossi's recollection, had two thread-like appendages on the prothorax.

We have to acknowledge with hearty thanks the pains bestowed upon the plates by Mr. Hammond, who has, among other things, materially improved and corrected our drawings of the larval head.*

* Since our paper was read there has appeared in the Lunds Universitets Årsskrift, xxxiii., an account of the larva of *Phalacrocera*, by Simon Bengtsson. The plates give useful information respecting the external features, the mouth-parts, and the skeleton of the head. Our ignorance of Swedish prevents us from making more than a superficial acquaintance with the text.

REMARKS ON THE LITERATURE OF THE EARLIER STAGES OF THE CYLINDROTOMINA, A SECTION OF THE TIPULIDÆ.

By Baron C. R. Osten Sacken, Hon. F.E.S.

In the Monograph of North American Diptera, iv., pp. 289–308 (1869), in giving an account of the Section Cylindrotomina, I introduced whatever was known about their life-history at that time. Very little has been added to our knowledge since. What I have done now is to overhaul the existing literature for a second time, and to prepare a detailed digest of it, arranged under the headings of the three principal genera of the section. It will be seen that with this mode of treatment the peculiarities of the larvæ and pupæ of the Cylindrotomina are brought out with more distinctness than they were in my work of 1869, and that these peculiarities fully bear out the intermediate position which I have given to that section between the *Tipulidæ longipalpi* and *brevipalpi*. This intermediate position has been further justified by the discovery that, during the Oligocene period in Western North America, the Cylindrotomina were, apparently, much more common than now, and that, for this reason, they may be considered as the ancestral form among the present Tipulidæ. Many specimens were found in the fossiliferous strata about Florissant, Colorado, and the White River, Utah. Whether they represent as many species as Mr. Scudder makes out of them, remains to be seen. (Compare Scudder, Tertiary Tipulidæ, Proc. Am. Phil. Soc., xxxii., 1894.)

The three genera of Cylindrotomina, about the transformations of which I reproduce the (in one case hypothetical) literature, are :—*Phalacrocera*, Schin., *Cylindrotoma*, Macq., and *Triogma*, Schin. The life-history of the genus *Liogma*, introduced by me (Monogr., iv., p. 298, 1869), is as yet unknown.

1. Phalacrocera, Schin.

De Geer (Nova Acta Upsal., i., pp. 66–77, Tab. 6 (1773); Mém. Hist. Ins., vi., p. 351, Tab. xx., figg. 1–16 (1776).—An excellent description of the external form and habits of the larva, pupa, and imago of *Phalacrocera replicata*, Linn.

Grube (Jahresb. d. Schles. Ges. für Vaterl. Kultur, 1867, p. 59).—A rather detailed description of evidently the same larva, but not identified.

Engel (Ent. Nachr., 1884, p. 260).—Short notice of the discovery by him of the same larva upon the stems of *Ranunculus fluitans*, in a lake, in the vicinity of Frankfurt-on-the-Oder.

Giard, Prof. A. (Bull. Soc. Ent. France, 1895, p. ccxxxv.).—An interesting notice of the same larva, which he found in pools of water among the downs between Wimereux and Ambleteuse (Dépt. Pas de Calais), hidden in the aquatic moss, *Hypnum elodes*, Spruce. He quotes a number of other continental stations.

2. Cylindrotoma, Macq.

Schellenberg (Genres des Mouches Diptères, Zürich, 1803).—In French and German. Tab. xxxvii., fig. 1, represents a *Tipula*, wrongly named in the corresponding letter-press (pp. 22–23) *Tipula histrio*, Fabr. As I pointed out in 1869 (Mon., p. 299), the figures of the larva and pupa make it evident that the species is *Cylindrotoma distinctissima*, Meig. The text merely says, "We know this larva, which has been found on *Viola bijlora*, Linn.; we shall give its history in another place." This promised publication has, to my knowledge, never appeared.

Boie (Kröyer Naturh. Tidskr. ii., p. 234, 1838; half a page).—Boie did not know of Schellenberg's publication. He gives a short description of the larva and pupa, which answers to Schellenberg's figures. He adds: "It deserves to be noticed that the *green* colouring of the larva indicates quite a different mode of life from that of other Tipulidæ. Numerous congregations of them were

observed gnawing the leaves of *Stellaria nemorum* in shady places among woods about the end of August. The transformation took place on the stems of the plants, to which the pupæ adhere by the tail, just like the chrysalids of butterflies. The fly develops about the middle of September."

Zeller, P. C. (Dipterologische Beiträge, 2te Abth., Isis, 1842, pp. 807–809.—*Limnobia distinctissima*, Wied., Meig.). Zeller refers to Boie, but deems it useful to give a more detailed description. He found the larvæ near Glogau (Silesia) in the spring, on leaves of *Anemone nemorosa*; in some places they occurred abundantly. The larvæ generally remain on the underside of the leaves, and by gnawing, make holes in them. About the middle of May they leave their food plants, fasten themselves upon grass-blades, leaves, etc., and usually pupate on the very next day; the pupæ show a remarkable analogy to those of the genus *Pterophorus* (Lepidoptera). They hang fastened by the tail of the larva-skin, which is not stripped off the last three or four segments. Zeller gives a more detailed description of the larva and pupa than his predecessors. It results from the preceding statements that the larva of *Cyl. distinctissima* occurs on various phanerogamous plants—*Viola*, *Stellaria*, and *Anemone*, and that it has, at least in some localities, *two* generations, one in the spring (Schellenberg, Zeller) and the other in autumn (Boie).

3. The supposed larva of Triogma.

G. de Rossi (Ent. Nachr. 1876, pp. 30, 31) describes a peculiar larva which he had discovered in woods, upon a species of moss (*Hypnum*), among which it was hidden. He succeeded in rearing the pupa, but unfortunately the pupa produced only an Ichneumon. As he had not made a description of the larva before its pupation, he published an account of it from memory. In this account I recognised the larva of a Tipulid belonging to the Section Cylindrotomina. A short article, which I published about it in the same periodical (Ent.

Nachr. 1878, p. 5), contains the following statement:—"The three-fold branches of the thorn-like processes (die dreifach verästelten Dornen) of the larva of De Rossi, remind one of the aquatic larva described by De Geer, and as this new larva seems to hold the middle place between the terrestrial larva of *Cylindrotoma* and the aquatic one of De Geer, it seems to me possible and even probable, that it may belong to a third of the known genera of the Section Cylindrotomina, *Triogma*. This supposition seems to be supported by the fact that this larva, like the aquatic larva of *Phalacrocera*, feeds upon a species of moss (*Hypnum*), differing in this from the larva of *Cylindrotoma*, which, as we have seen, occurs on different kinds of phanerogamous plants."

In the Monograph of North American Diptera, iv., pp. 289–292, I have shown that the Cylindrotomina occupy an intermediate position between the two great, and otherwise very well defined, divisions of the Tipulidæ, the *longipalpi* and *brevipalpi*. And I have called attention (*l. c.* p. 295) to the anomalous character of their larvæ, corresponding with that of the perfect insects. Larvæ climbing upon living plants, feeding upon them, and gnawing holes in their leaves, are *toto cœlo* different from ordinary larvæ of Tipulidæ. These larvæ must of course show corresponding adaptations for such a mode of life, and it will be the task of future investigators to describe these structural differences in detail. What we can gather from the existing descriptions is very little, and is found principally in Zeller. According to him, climbing is made possible by sucking-cups, the principal one of which is produced by the withdrawal of the head into the thoracic segments, thus forming a hollow, the edges of which complete the cup. He believes that eight pairs of conical, fleshy protuberances on the ventral side when withdrawn, may likewise act as sucking-cups for locomotion. Zeller's statement about the breathing apparatus proves that the larvæ of *Cylindrotoma distinctissima* are *metapneustic*, like those of *Phalacrocera* and other Tipu-

lidæ. He says—"The translucent tracheæ end, a short distance from the anus, on the dorsal side, in two brown, very distinct spiracles; their anterior end is not visible, because, in the anterior segments, they lie deeper from the surface."

The pupæ of the Cylindrotomina are also very peculiar; they are fastened to the food plants, and resemble the pupæ of some Lepidoptera.

PLATES VIII.–XI.

[*The explanation faces the* PLATES.]